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The nomenclatural history of *Umbilicaria spodochoa* and nomenclatural corrections in *Umbilicariaceae*

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ABSTRACT—The name *Umbilicaria spodochoa* is currently applied to a species with an oceanic distribution in Europe and East Asia. The upper surface of its thallus is grey to dark brown, apothecia are omphalodisc, with a prominent central umbilicus-like button. Its designated type and other original material are referable to *U. hirsuta*. Conservation is required to retain this name in current use. The nomenclatural history of *U. spodochoa* is presented to serve as the background for its conservation. The subgeneric nomenclature of *Umbilicaria* is revised and one new name (*U. subg. Papillophora*) is proposed to replace the illegitimate *U. subg. Gyrophora*. The status of many new names published by G.F. Hoffmann in his 'Deutschlands Flora' (1796) is discussed and their nomenclatural validity is supported.

KEY WORDS—conservation, Ehrhart, historical collections, Hoffmann, typification

Introduction

Species of *Umbilicariaceae* Chevall. are predominantly saxicolous lichens mostly found in regions of higher latitudes or altitudes worldwide. Multilocus phylogenies resulted in a new generic concept of the family, which currently includes three genera comprising together about one hundred species of mostly umbilicate growth habit (Bendiksby & Timdal 2013; Davydov & al. 2017).

Morphological details of the upper and lower thallus surfaces as well as traits of the rhizinomorphs were mostly taken into consideration by earlier lichenologists to distinguish different species of *Umbilicaria* Hoffm. However, these characters have not always been easily recognizable. For this reason, the circumscriptions of some of the early described species have been controversially discussed. One of the species with a rather complicated taxonomic and nomenclatural history is *Umbilicaria spodochoa*, which was often confused with another early described species, *U. hirsuta* (Sw.) Ach., in the 18th and 19th centuries.

Umbilicaria spodochoa, with an oceanic distribution in Europe and East Asia (Wei & Jiang 1993), is characterized by a large thallus with a grey to dark brown and upper surface and pale brown to black papillate lower surface with abundant rhizinomorphs and characteristic, omphalodisc apothecia with prominent central umbilicus-like button. By such characterization, this species is easily recognizable and specimens thereof were frequently distributed in exsiccatal series (see the list in Llano 1950).

Umbilicaria hirsuta, a Holarctic species, is characterized by producing parasoredia on the marginal part of the upper thallus surface, unlike the closely related *U. grisea* Hoffm., on which the parasoredia clump and become farinose with granules of various size (Codogno & al. 1989). The lower surface of *U. hirsuta* is beige to almost black with sparse to abundant rhizinomorphs. Apothecia are rarely produced and belong to the gyrodisc type.

As currently defined (Frey 1933; Llano 1950; Codogno & al. 1989; Wei & Jiang 1993), the latter two species can be unambiguously distinguished by their diagnostic characters as stated above. Both species names are currently accepted (Poelt & Vězda 1981; Hitch & Purvis 2009; Stenroos & al. 2016), and the species were assigned to the recently resurrected ‘*Umbilicaria* subg. *Gyrophora* (Ach.) Frey’ (Davydov & al. 2017), which corresponds to a rather large clade of 13 species that have been phylogenetically analysed. The core of this clade is constituted by the *Umbilicaria vellea* group, which includes *U. spodochoa* and *U. hirsuta*.

In spite of the current advances in the taxonomy of *Umbilicariaceae*, the nomenclature of several species is still to be clarified. In the present contribution we aim at unravelling the old confusion concerning the species name *Umbilicaria spodochoa*.

Materials and methods

The protologue of *Umbilicaria spodochoa* and the relevant historical literature was examined to uncover the history and the original material of the name. Herbarium collections as well as high resolution digital photographs of *Umbilicaria* from GOET, H, LE, LINN, MW were studied, de visu, or via online portals (<https://plants.jstor.org>), or provided by curators. Taxonomic literature was screened for relevant treatments.

Historical background

A species of *Umbilicaria* with the specific epithet “spodochrous” was first introduced by Ehrhart (1793), who distributed a specimen named

“*Lichen spadochrous* Ehrh.” in his *exsiccatae* (FIG. 1). The specimen was accompanied with a printed label but no description or diagnosis of the species was provided.

The species epithet is controversial because in its original spelling it is meaningless and has been considered linguistically erroneous for long (e.g., Schade 1955). Nylander (1861: 115; 1869: 11) stated that the epithet ‘spadochrous’ seems to be a misspelling because it is apparently derived from the Greek word σποδός (cinder), meaning ‘ashes’. Since the species epithet was incorrect, either **as a typographic or orthographic error**, its spelling may be corrected to ‘spodochrous’ under Art. 60.1 (Turland & al. 2018), which is currently in common use.

Acharius (1794) referred Ehrhart’s specimen of ‘Lichen spadochrous’ to *L. polyrhizos* L. This was done under a broad species concept and made no practical implications to the further taxonomy and nomenclature.

Valid publication and protologue

Hoffmann (1796) revised species of cryptogams (ferns, mosses and lichens) known from Germany. Since the available knowledge was very uneven and several taxa were not sufficiently understood at that time, he treated the taxa differently as he explained in the Preface:

“Varietäten, Halbarten (Subspecies), auch Arten, welche ich als solche aufzuführen noch unentschlossen war, findet man entweder in Klammern () den Anmerkungen, oder ohne Bezifferung der nächstverwandten Art beigestellt” [= Varieties, subspecies, also species that I was still undecided to list as such, are to be found either in brackets () placed with the annotations, or, without numeration, with the most closely related species] (Hoffmann 1796: [Vorbericht: 4]).

In the Index, according to our interpretation of this work, Hoffmann (1796) implicitly listed accepted names and their basionyms in italics and synonyms in the regular font. In the taxonomic part of his work, he listed many species without numbers, yet with binomial names in the accepted genus. Several of such species were new to science. In annotations placed in brackets, Hoffmann mentioned quite a number of species names published by previous authors, with their original generic assignments. He also mentioned several varieties in these annotations, usually unnamed or under old polynomials, sometimes with previously published species names; according to the Index, such species names were listed as synonyms. Hoffmann’s use of subspecies was very sparse, and we are not aware of any name that he may have applied at this rank.

Isoviita (1966) considered new names in Hoffmann's treatments of 'undecided' taxa invalidly published because of the presumed absence of explicit acceptance by the author (Art. 36.1). Contrary to his opinion, we consider the internal evidence in Hoffmann (1796) (typesetting of the Index and explanations in the Preface) to be sufficient to dispel doubts about Hoffmann's acceptance of such taxa.

Hoffmann (1796) was the first to provide a description for Ehrhart's lichen under the name '*Umbilicaria spadochroa*'; although this species name was left unnumbered in the synopsis, it was listed as accepted in the Index and therefore was validly published in spite of any doubts that Hoffmann may have had at that time.

The species description provided by Hoffmann is inadequate to distinguish between the species of *Umbilicaria* in their current circumscription. Hoffmann distinguished *U. spadochroa* from its presumed closest relative *U. hirsuta* mostly by the colour of the upper thallus surface (bluish grey vs. grey) and the lower thallus surface (light brown vs. brownish grey), and also by the density of rhizinomorphs (scarce vs. abundant). These characters are variable in both species in that the colour of the lower thallus surface varies from beige to black-brown and the rhizinomorphs are scarce to abundant. According to the current species concept, Hoffmann's description fits both taxa, *U. spadochroa* and *U. hirsuta*, so that it can be applicable either to a species different from *U. hirsuta* or it may indicate a phenotypic variation within the same species.

Further treatments

A later author who treated this lichen species was Acharius (1799), who validly published the combination *Lichen spadochrous* (as 'spadochrous'), which was explicitly accepted and accompanied by a species description. Acharius broadened the limits of this taxon and, disregarding priority, included one previously described species, *Umbilicaria cirrosa* Hoffm.; this name has not yet been typified but the figures accompanying the description by Hoffmann (1789) suggest that it may be a synonym of *U. vellea*.

Acharius (1799, 1803) specified the character of the lower surface of the thallus as dark hirsute ("subtus ater hirsutus"). Later, Acharius (1810: 673) emphasized that his *Gyrophora vellea* (L.) Ach., *G. spadochroa*, and *G. crustulosa* Ach. can be optimally distinguished by their apothecial morphologies. In this work, Acharius was the first to mention one of the most important diagnostic characters of *Umbilicaria spadochroa*, i.e., the prominent central button on the apothecia. Finally Acharius (1814) lowered

the rank of the taxon to the varietal level but maintained its diagnostic characters.

It is rather obvious that the works of Acharius were essential in establishing the current concept of *U. spodochoa*. Nevertheless, despite the characters indicated in his descriptions the specimens labelled by Acharius as “*Gyrophora vellea* β *G. spadochoa*” belong to *U. vellea* (H-ACH 581) or *U. vellea* and *U. cinereorufescens* (Schaer.) Frey (H-ACH 580). The specimens referable to *U. spodochoa* were identified by Acharius as “*Gyrophora vellea*” (H-ACH 576), in accordance with the illustration of the latter species in Acharius (1794: Tab. III, fig. 3).

The same type of apothecia, with thick margin and a central verruca, was described for *Umbilicaria vellea* var. *spodochoa* by Stenhammar (1825), although the respective herbarium specimen was referable to *U. vellea* (Merrill 1906). The other important diagnostic characters of the species were unknown by that time.

Nylander (1861) established an additional character that can be used as diagnostic for *Umbilicaria spodochoa*: the ascospores being simple and colourless to submuriform and brown. However, he treated this species broadly and included other taxa of *Umbilicaria* with submuriform ascospores: *U. cinereorufescens*, *U. cirrosa*, *U. crustulosa* and *U. depressa* (Ach.) Duby (Nylander 1869).

The broad concept of *Umbilicaria spodochoa* prevailed until Frey (1933) recognized the four aforementioned species as separate and provided an artificial key and detailed descriptions, which are still acceptable. Frey's treatment became the basis for all subsequent interpretations of *U. spodochoa* and established the current application of its name.

Type designation

Hoffmann (1796) cited two collections in the protologue, which are therefore syntypes. The first collection is “*Lichen spadochrous*” of Ehrhart (1793), which was erroneously cited under no. 317 instead of no. 316. The distribution of Ehrhart's exsiccatae was so limited (Gubanov & Balandina 2000) that this incorrect citation was reproduced in the great majority of subsequent taxonomic publications.

We were able to locate three specimens of Ehrhart's “*Lichen spadochrous*”, at GOET, LINN-HS and MW. In addition we checked B, BM, G, HAL, LE, M, and UPS, i.e., the herbaria in which some Ehrhart's collections are known to be located, but without success.

The specimen at GOET (barcode 019934) was studied by Arnold (1880) and Schade (1955), who referred it to *Umbilicaria hirsuta*. We agree with

this identification because of its prominent marginal farinose-granular parasoredia.

The specimen at LINN-HS (1703.19.3) belongs to the Herbarium of Sir James Edward Smith, to which it went through the collection of Edmund Davall in 1802 (Beer 1947). According to the annotations, Smith referred it to '*Lichen polyrrhizos*', and its correct identity is *Umbilicaria hirsuta*.

The specimen at MW belongs to the personal collection of F. Ehrhart, which was owned by Hoffmann who left its part, including sets of the exsiccatae, to the Moscow Branch of the Military Medical-Surgical Academy, from which the collections were transferred to the Moscow University after the Academy was closed in 1842 (Sokoloff & al. 2002). Some specimens of Ehrhart's cryptogams were purchased by the Botanical Museum of the St. Petersburg Academy of Sciences (now the Komarov Botanical Institute) (Karavaev & Barsukova 1968) but the specimen of "*Lichen spadochrous*" was left in Moscow (Gubanov & Balandina 2000). This specimen was certainly examined by Hoffmann and apparently was the main basis for the original description and his concept of *Umbilicaria spodochoa*. The traits of his specimen fit well to the original description, but it evidently also belongs to *U. hirsuta*.

The second collection mentioned by Hoffmann (1796) is a specimen of '*Lichen polyrrhizos*', which was communicated by Smith. We cannot recognise this specimen among the lichen collections of Hoffmann, which were purchased from him by the Moscow University (Hoffmann 1825). However, a suitable specimen in Smith's herbarium (LINN-HS 1273.212), identified as '*Lichen polyrrhizos*' and originating from Ehrhart's collection, matches the protologue of *Umbilicaria spodochoa*. This specimen, which was received by Smith most likely in 1793 (as evident from annotations on other similar specimens in this collection, e.g. LINN-HS 39.34) and may have been shared with Hoffmann prior to 1796, could be part of the gathering mentioned by Hoffmann in the protologue. This specimen also belongs to *U. hirsuta*.

The original description of *Umbilicaria spodochoa* and the relevant herbarium material convincingly demonstrate that this name was applied by Hoffmann to a variant of *U. hirsuta*, not to the species known as *U. spodochoa* in the current use. Arnold (1880) studied Ehrhart's lichen collections and stated that Ehrhart's specimen of "*Lichen spadochrous*" was mixed and the typical *U. spodochoa* was also present under no. 316; however, we have found no evidence for this statement. Moreover, *U. hirsuta* is common in the vicinity of Uppsala Uppsala (Shah & Coulson 2018), the type locality of *U. spodochoa*, but *U. spodochoa* in the current use is absent from Uppsala itself, although it occurs fairly close to the town, mostly

along the coast and to some extent along the shores of Lake Mälaren (S. Ekman, pers. comm.).

Llano (1950: 101) rather mechanically cited “Ehrhart ... Crypt. Exs. 317” as the type of *Umbilicaria spodochoa*, thus fulfilling conditions for effective type designation (Art. 7.11, 9.17). This typification is formally correct but has an undesirable effect that a familiar species name would change its application because the type collection belongs to *U. hirsuta* but the species name has been used in the sense of *U. spodochoa* widely and persistently since Frey (1933). Llano’s type designation is referable to a gathering rather than a specimen, since he failed to specify the herbarium in which the type is housed, but we refrain from the second-step typification of the name as unnecessary in view of a conservation proposal currently under review (Hestmark, submitted).

Umbilicaria spodochoa Hoffm., Deutschl. Fl. 2: 113. 1796, [as “*spadochoa*”]

≡ *Lichen spodochrous* (Hoffm.) Ach., Lichenogr. Suec. Prodr.: 149. 1799 [“1798”; as “*spadochrous*”]

≡ *Gyrophora spodochoa* (Hoffm.) Ach., Methodus: 108. 1803 [as “*spadochoa*”]

≡ *Gyrophora vellea* var. *spodochoa* (Hoffm.) Ach., Syn. Meth. Lich.: 68. 1814 [as “*spadochoa*”]

≡ *Umbilicaria vellea* var. *spodochoa* (Hoffm.) Stenh., Sched. Crit. Lichen. Suec. 5–6: 4. 1825 [as “*spadochoa*”]

≡ *Omphalodiscus spodochrous* (Hoffm.) Schol., Nyt Mag. Naturvid. 75: 26. 1934

LECTOTYPE (designated by Llano 1950: 101): Sweden. Uppsala, F. Ehrhart in Plantae Cryptogamae Linn. no. 316 (GOET [image!], LINN-HS [image!], MW [image!]).

Subgeneric nomenclature

Gyrophora Ach. was published as an explicit substitute (replacement name, Art. 6.11) for the illegitimate *Umbilicaria* Hoffm. 1789 (non Fabr. 1759), even though the illegitimacy of Hoffmann’s genus was not realized at that time (e.g., Leighton 1856). Acharius (1803: 100) cited Hoffmann’s name in synonymy and stated that he changed the latter because he considered it “not optimal”, thus making both names homotypic (Art. 7.4). Since the generic name *Umbilicaria* Hoffm. was illegitimate prior to its conservation in 1996 (Art. 14.15), the autonym “*Umbilicaria* subg. *Umbilicaria*” cannot be established (Art. 22.5); because of the illegitimacy of the generic name, Art. 22.2 does not apply and the combination *Umbilicaria* subg. *Gyrophora* (Ach.) Frey was validly published for a subdivision of the genus that includes the type of the generic name. When Davydov & al. (2017) accepted *U.* subg. *Gyrophora* but excluded from its circumscription the type of *Umbilicaria*

(which is also the type of *U.* subg. *Gyrophora* (Ach.) Frey), and also provided a description of this subgenus and a type designation, they created an illegitimate later homonym (Art. 48.1), which however was not validly published under Art. F.5.1. This subgenus is formally named here with the same type and a reference to the validating description in Davydov & al. (2017).

Two other subgeneric names accepted by Davydov & al. (2017) are revised with their corrected nomenclature as follows.

Umbilicaria* subg. *Agyrophora Nyl. [Flora 61: 247. 1878, nom. nud.] ex Cromb.,
Monogr. Lich. Britain 1: 323. 1894
TYPE (designated by Llano 1950: 49): *Umbilicaria atropruinosa* Schaer. [= *Umbilicaria leiocarpa* DC.]

Umbilicaria* subg. *Lasallia (Mérat) Frey, Hedwigia 71: 106. 1931
= *Lasallia* Mérat, Nouv. Fl. Env. Paris, ed. 2, 1: 202. 1821
TYPE: *Umbilicaria pustulata* (L.) Hoffm.

Umbilicaria* subg. *Papillophora Davydov, Ahti & Sennikov, **subg. nov.**
MB 830067

VALIDATING DESCRIPTION: under *Umbilicaria* subg. *Gyrophora* “(Ach.) Frey”,
Taxon 66: 1297. 2017

TYPE: *Umbilicaria vellea* (L.) Ach.

ETYMOLOGY. The name refers to the papillose lower surface and rhizinomorphs, the characteristic trait for the majority of species in the subgenus.

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Norbert Kilian (Berlin) kindly commented on the complicated taxonomy and nomenclature of Hoffmann (1796), and provided his English translation of the quoted passage. We are grateful to Marc Appelhans (Göttingen) for scanned images and a photocopy of the printed matter of Ehrhart’s exsiccatae from GOET. Mikhail Kozhin (Moscow) supplied a photograph from Ehrhart’s collection at MW. The following curators kindly reported the absence of Ehrhart’s specimens: Stefan Ekman (UPS), Uwe Braun (HAL), Andreas Beck (M), Robert Lücking (B), Philippe Clerc (G), Len Ellis (BM). Stefan Ekman is also thanked for information on the occurrence of the species of *Umbilicaria* around Uppsala. A photograph of *Umbilicaria spodochoa* from GOET is reproduced with kind permission from the Georg-August-Universität Göttingen.

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FIGURE 1. Type collection of *Umbilicaria spodochoa*, voucher from Göttingen (GOET 019934). A. printed label of Ehrhart's exsiccata; B. upper surface of thallus; C. lower surface of thallus. Photo: Marc Appelhans.